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Ecology and Management of the Bullfrog

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Front cover photo.
The adult bullfrog (*Rana catesbeiana*) is the largest and most economically important frog of North America. *Photo by J. T. Collins.*

ECOLOGY AND MANAGEMENT OF THE BULLFROG

By R. Bruce Bury
Jill A. Whelan

> "Each of us has actually before him, or in memory, a typical pond or small lake, for our country is every-where made picturesque by them. The lilies make up a large part of its beauty, the Bullfrog a large part of its life. The Bullfrog is the spirit of the place. Independent, self-composed, silent, he may sit for hours with no slightest movement to tell that he is alive. But he is fully alert to every disturbance of the water and to every shifting shadow."
>
> Dickerson (1906)

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Ecology and Management of the Bullfrog

by

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Abstract

The bullfrog (*Rana catesbeiana*) occurs throughout the central and eastern United States and into southern Canada, one of the largest geographic ranges of any North American amphibian. This frog has been widely introduced into almost every State in the United States and into several foreign countries. The bullfrog is prized as food, and there are large sport and commercial harvests of wild frogs annually. Some frogs also are sold for scientific and educational use. Bullfrog culture in private ponds was once advocated as a money-making venture, but no frog farm has demonstrated sustained operation. Intensive culture efforts are costly and economically unproved to date, but some technological improvements are being made experimentally. Although bullfrogs are a major game species, management of wild stocks is minimal. Many wild populations seem to be declining and the reasons for the decreases are unknown. In nature, the bullfrog is a large-bodied, opportunistic omnivore which in turn provides food for many other species of wildlife.

This paper summarizes and critically reviews information on the biology of the bullfrog (*Rana catesbeiana*) related to its ecology, present status, culture, and management. Most of the literature used in our review was located in the libraries of the Division of Reptiles and Amphibians, Smithsonian Institution, and the U.S. Department of the Interior, Washington, D.C. We selected information through 1982 representing the most recent, important biological and economic features of the bullfrog, but we also include historic references where such information is pertinent.

Description

The bullfrog (*Rana catesbeiana*) is a familiar denizen of North America. In 1694, Clayton (*in* Holbrook 1842) described it as a large frog, "bigger than any in England, which makes a noise something like the bellowing of a bull." The bullfrog is part of American folklore and was probably among Mark Twain's fabled jumping frogs of Calaveras County, California (Storer 1925; Bury and Luckenbach 1976).

Bullfrogs are the largest North American frogs (Fig. 1); males measure about 180 mm long and females about 200 mm (Wright and Wright 1949; Stebbins 1954, 1966; Conant 1975), although even longer bullfrogs have been found in California (Treanor and Nichola 1972).

Bullfrog tadpoles are exceptionally large, reaching lengths of 152-178 mm (Dickerson 1906; Wright and Wright 1949; Altig 1970). They have a green or olive dorsum with a straw- or maize-colored belly, mottling over the body, and many small dark spots and fine yellow dots (Fig. 2). Keys for identifying tadpoles are provided by Orton (1951) and Altig (1970).

Juvenile bullfrogs are usually olive-green with black dots covering the dorsum (Wright and Wright 1949; Smith 1961). Adults are olive, green, or brown above, but may vary from yellow-green to black. Phillips and Boone (1976) reported yellow bullfrogs in central Pennsylvania. The legs are banded and blotched and there is variable spotting and mottling on the back (compare cover photograph with Fig. 1). The underside is white mottled with gray.

The head of the bullfrog is broad and flat. The bullfrog has well-developed tympanic folds but, unlike most North American *Rana*, no dorso-lateral folds. The tympanum of full-grown males is larger in diameter than the eye and is dark brown marginally; the tympanum of adult females is about the same size as the eye. This difference becomes apparent after the

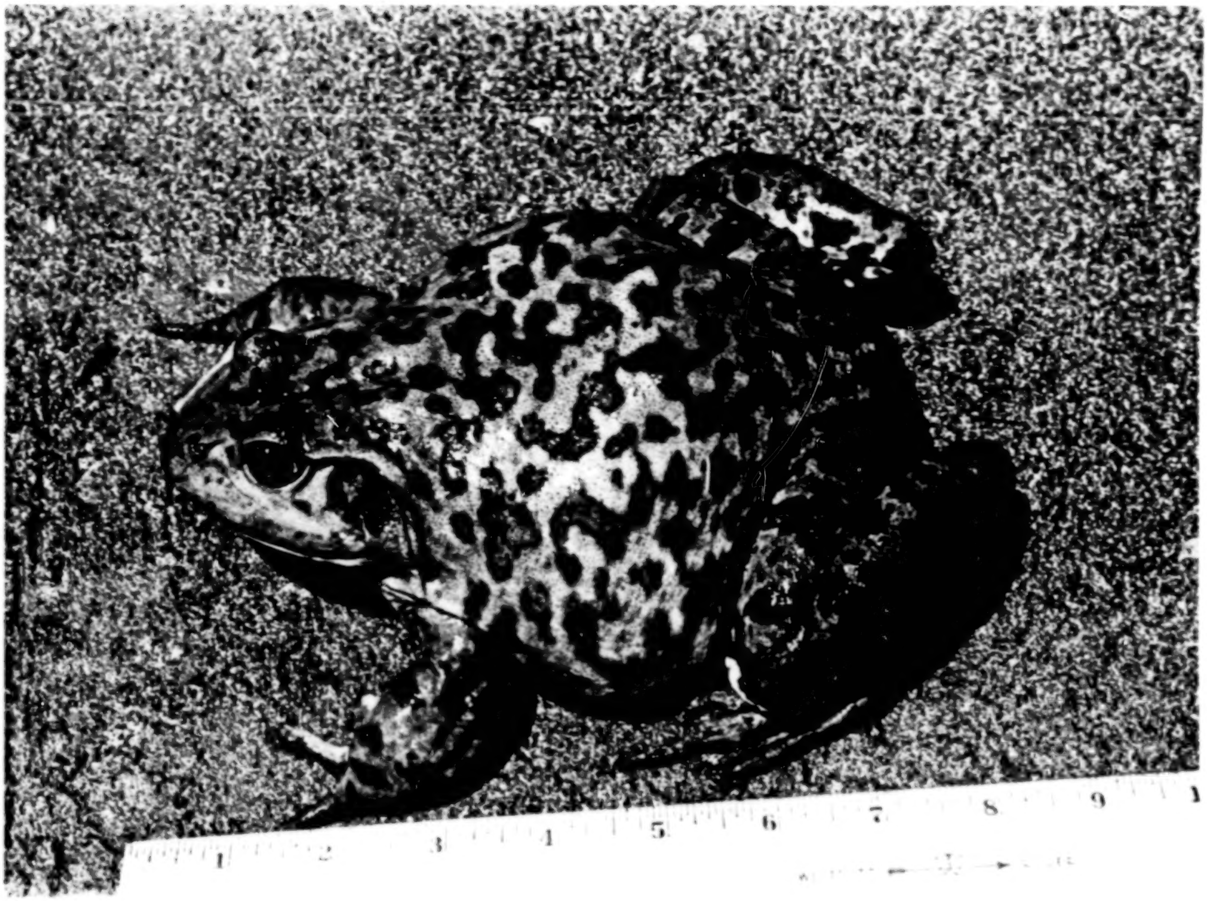

Fig. 1. Large adult bullfrog from California. Note the considerable amount of dorsal mottling. *Photo by J. M. Brode.*

frogs reach sexual maturity (George 1938, 1940; Schroeder and Baskett 1968). Males have swollen thumbs and yellowish throats (Ruffner 1933; Stebbins 1954, 1966; Conant 1975).

Geographic Range

Bullfrogs have occurred naturally from Nova Scotia south to central Florida and westward across the Great Plains (Wright and Wright 1949; Stebbins 1954, 1966; Conant 1975). Kellogg (1932) reported that bullfrogs in Mexico were probably restricted to the coastal lowlands of Tamaulipas and northern Vera Cruz, and to the tributaries of the Rio Grande River in northern Mexico.

The limits of natural range are now hopelessly confused because bullfrogs have been widely introduced into the western United States and elsewhere (Fig. 3). For example, bullfrogs were introduced in California between 1905 and 1915 (Cohen 1975); they are now widespread throughout the State (55 of 58 counties; Bury and Luckenbach 1976) and, in many areas, are the most common frog (Storer 1922, 1933; Sloan 1964; Moyle 1973). The original range of bullfrogs in Nebraska is thought to have included only river bottom and river oxbow areas in the eastern half of the State; their present establishment over much of the State is probably due to incidental introduction with the stocking of fish (McAuliffe 1978). Other introduced populations occur in British Columbia (including Vancouver Island), Mexico, the Caribbean Islands, Brazil, the main Hawaiian Islands, the Far East, and Europe.

Within their original range bullfrogs were naturally limited in their distributions (Moore 1942; Bleakney 1958). In eastern Canada, Bleakney (1958) reported the species only in southern Ontario and Quebec. Bullfrogs occur naturally in western Wisconsin (Vogt 1981), but they seem to be absent from Minnesota and North Dakota (Wheeler and Wheeler 1966; Conant 1975), and are marginal or poorly established in South Dakota (Fishbeck and Underhill 1959, 1960; Smith et al. 1966) and Montana (Black and Bragg 1968; Black 1969). Ellis and Henderson (1913), Van Denburgh (1924), and Wright and Wright (1949) did not report the bullfrog in Colorado and New Mexico; recent reports from these

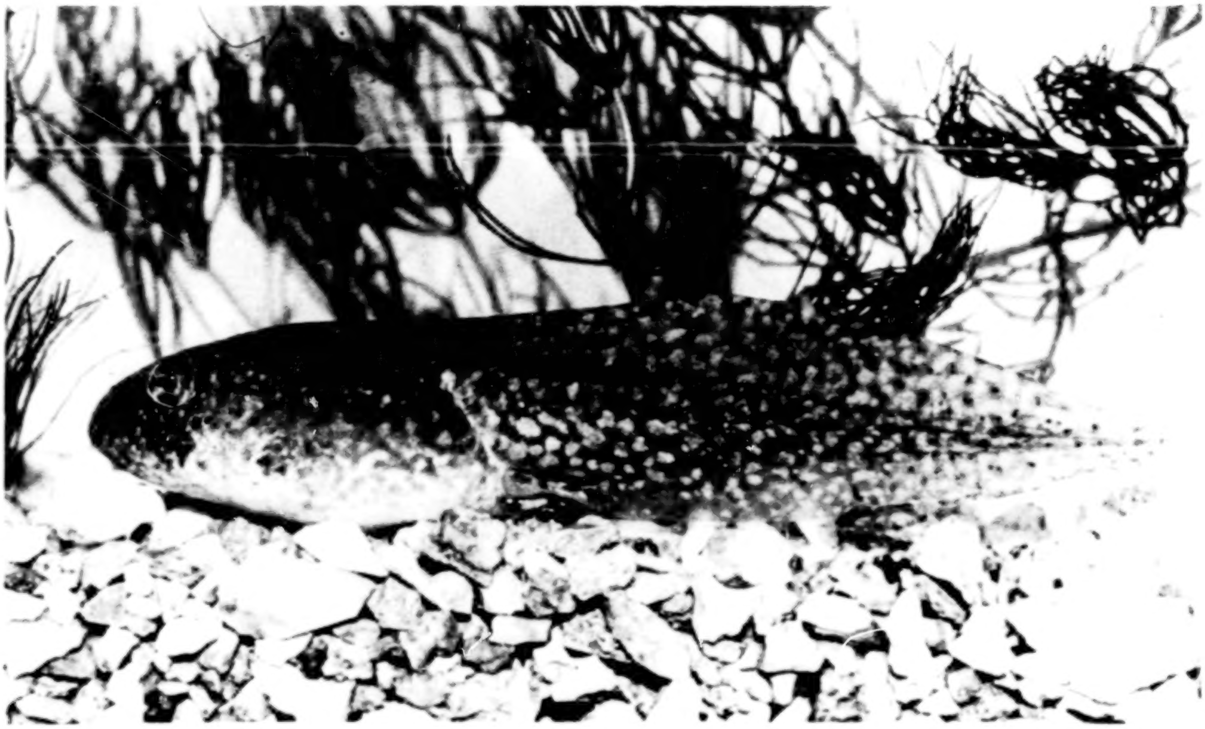

Fig. 2. Tadpole of the bullfrog. *Photo by T. R. Johnson; courtesy of the University of Kansas.*

States are probably a reflection of bullfrog introductions. In Texas, the bullfrog was probably absent naturally from the Edwards Plateau, southern Texas south of Nueces County, and the Trans-Pecos region (Raun and Gehlbach 1972). Recently, Neck (1981) suggested that the species occurred earlier near the Nueces River in south Texas. There are now well-established populations (probably introduced) in the plains and prairie regions of Wyoming (Stebbins 1954; Conant 1975; Baxter and Stone 1980), Nebraska (Hudson 1942; Gehlbach and Collette 1959; McAulifte 1978), Colorado (Maslin 1959, 1964; Smith et al. 1965; Hammerson 1982*a*); Kansas (Smith 1934, 1950; Clarke et al. 1958; Collins 1974, 1982), and Texas (Raun and Gehlbach 1972).

Reports on introductions are provided by Van Denburgh and Slevin (1921); Storer (1922, 1925, 1933); Wright and Wright (1949); Anonymous (1952); Stebbins (1954, 1966); Oliver (1955); Sloan (1964); Hardy and McDiarmid (1969); Culley and Gravois (1970); Raun and Gehlbach (1972); Treanor and Nichola (1972); Cohen (1975); Conant (1975, 1977); Schwartz and Thomas (1975); Mullen (1976); Mahon and Aiken (1977); Fitzner et al. (1978); Green (1978); McKeown (1978); Baxter and Stone (1980); and Hammerson (1982*a*, 1982*b*).

Habitat

Bullfrogs are mostly aquatic and require a permanent source of water. Preferred habitats are vegetated shoals, sluggish river backwaters and oxbows, farm ponds, reservoirs, marshes, and still waters with tules, dead trees, snags, and twisted roots (Holbrook 1842; Dickerson 1906; Storer 1922, 1925; Breckenridge 1944; Wright and Wright 1949; Stebbins 1954; Smith 1961; Treanor and Nichola 1972; Collins 1974, 1982; Conant 1975; Mount 1975; Treanor 1975; Johnson 1982). Plant growth in bullfrog habitat is often dense and emergent; favorite areas are vegetated with pickerel weed, lily pads, cattails, sedges, berry vines, and willows. However, some populations thrive along open, shallow edges of reservoirs, cow ponds, wells, canals, gravel pits, and intermittent streams (Cohen and Howard 1958; Moyle 1973; Bury and Luckenbach 1976).

Bullfrogs occur over a broad range of conditions, from the continental climate (cold winter, hot summer) of the northern and central United States and southern Canada to semi-tropical environs in the southern United States and the Mediterranean climate of the western United States (Dickerson 1906; Storer 1922, 1933; Wright and Wright 1949; Stebbins 1954, 1966; Smith 1961; Treanor and Nichola 1972; Conant 1975;

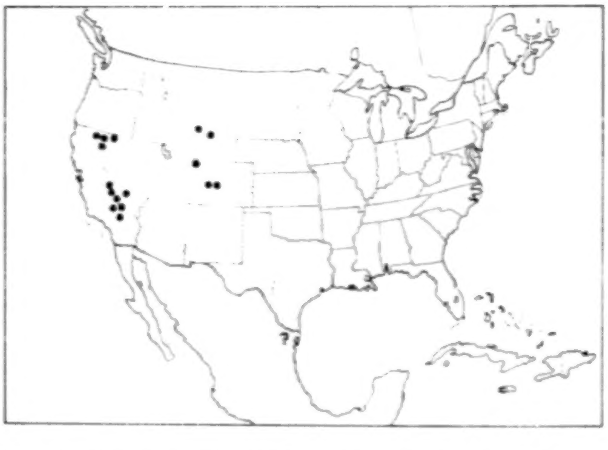

Fig. 3. Natural range (shaded) and areas of introductions (crosshatching and dots) of the bullfrog in North America.

Mount 1975). Populations may occur from sea level to elevations higher than 1,900 m but seem to be most abundant at lower elevations, particularly in habitats modified by man (Stebbins 1954, 1966; Moyle 1973; Conant 1975; Bury and Luckenbach 1976). In Colorado, Hammerson (1982*a*) found bullfrogs at 2,743 m, where warm spring waters enabled them to reproduce in an area that otherwise was much too cold. Some introduced populations survive in desert wells and springs (Turner and Wauer 1963; Bury and Luckenbach 1976), but may be extirpated by droughts (Blair 1957). Bullfrogs sometimes frequent underground caves or wells (Lee 1969; Mount 1975). Acidic waters (pH less than 4.2) seem to cause abnormalities in bullfrog tadpoles; thus, bullfrogs do not inhabit these waters (Gosner and Black 1957).

Foods and Feeding Behavior

Bullfrog tadpoles feed mainly on aquatic plant material and some invertebrates (Dickerson 1906; Wright and Wright 1949; Treanor and Nichola 1972). They may also be scavengers on dead fish or tadpoles (Dickerson 1906). In a laboratory study in Illinois using wild tadpoles, Ehrlich (1979) found that eggs and newly hatched larvae of *Rana blairi* were readily eaten by bullfrog tadpoles. Nevertheless, Funkhouser (1976) reported that California bullfrog tadpoles are so strongly herbivorous that they will starve in the presence of raw or cooked meat or fish food, and will not consume their own dead. Thrall (1972) found that bullfrog tadpoles are detritus feeders, and that algae did not seem to be of primary importance as food. D. D. Culley (personal communication) reported that tadpoles graze on small algae attached to a substrate, and Seale (1973) stated that ranid frog larvae graze on microscopic seston composed of algae, bacteria, and detritus. In a laboratory study, Steinwascher (1978) observed that bullfrog tadpoles that consumed their own feces grew larger than those that did not. Steinwascher's study needs confirmation because other food (e.g., seston on the glass) may have been present. There is no information on coprophagy in tadpoles in the wild.

Adult bullfrogs usually are "sit and wait" predators that readily attack almost any live animal smaller than themselves. Hobson (1966) reported that bullfrogs are immobile and clearly at rest for long periods of time, but they remain alert and react immediately to any external stimuli such as food, predators, or other moving frogs.

Adult bullfrogs feed on a wide variety of food (Table 1), including members of their own species (Dickerson 1906; Storer 1922; Viosca 1931; Smith 1950; Fulk and Whitaker 1969; Treanor and Nichola 1972). The bullfrog is notorious for its occasional consumption of relatively large animals such as mice, moles, bats, snakes, ducklings, and birds (Fig. 4). Some economically important prey are occasionally ingested. For example, we found a 15-cm-long trout (*Salmo* sp.) in the stomach of a bullfrog collected in a coastal lagoon in northern California. The bulk of the bullfrog's diet, however, is made up of crustaceans and insects (Dickerson 1906; Raney and Ingram 1941; Baker 1942; Wright and Wright 1949; Anonymous 1952; Korschgen and Moyle 1955; Cohen and Howard 1958; Bush 1959; Smith 1961; Korschgen and Baskett 1963; Schroeder and Baskett 1965; Taylor and Michael 1971; Minton 1972; Treanor and Nichola 1972; Carpenter and Morrison 1973; Pine 1975; McAuliffe 1978; Tyler and Hoestenbach 1979; Bruneau and Magnin 1980*b*; Corse and Metter 1980). In captivity, bullfrogs show a preference—in order of desirability—for tadpoles, fish, and crayfish (Culley and Gravois 1971).

Korschgen and Baskett (1963) found that the general feeding habits of Missouri bullfrogs were similar in large impoundments, in a river, and in farm ponds. The principal midsummer food was crayfish, followed in order of preference by insects, amphibians and reptiles, mammals, miscellaneous invertebrates, and fishes. In a study at a fish hatchery in southwestern Missouri, bullfrogs ate a wide variety of foods even though certain easily obtainable food items (i.e., goldfish, minnows) occurred in excess (Corse and Metter 1980). Bullfrogs ate fish throughout the year but their consumption of other foods varied seasonally. Crayfish appeared to be the preferred food and frog densities increased on ponds after they were infested with crayfish.

In Virginia ponds, insects and spiders were the most abundant bullfrog foods; male and female frogs ate similar foods, and vegetation was important in the diet (Brooks 1964). Frogs from Ohio ponds principally ate

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Table 1. *Foods of adult bullfrogs.*

Food	References
Vegetation	Perez 1951; Brooks 1964; Fulk and Whitaker 1969; Taylor and Michael 1971; Stewart and Sandison 1972
Earthworms	Surface 1913; Cohen and Howard 1958; Bush 1959; Korschgen and Baskett 1963; Brooks 1964; Fulk and Whitaker 1969; Stewart and Sandison 1972; Bruggers 1973
Leeches	Mahon and Aikens 1977
Insects	Holbrook 1842; Dickerson 1906; Hartman 1906; Surface 1913; Wright 1920; Storer 1925; Frost 1935; Raney and Ingram 1941; Breckenridge 1944; Wright and Wright 1949; Perez 1951; Cohen and Howard 1958; Bush 1959; Smith 1961; Korschgen and Baskett 1963; Brooks 1964; Schroeder and Baskett 1965; Fulk and Whitaker 1969; McLeran 1971; Taylor and Michael 1971; Minton 1972; Stewart and Sandison 1972; Treanor and Nichola 1972; Bruggers 1973; Carpenter and Morrison 1973; Mahon and Aikens 1977; McAuliffe 1978; Bruneau and Magnin 1980*b*; Corse and Metter 1980
Centipedes and millipedes	Bush 1959; Korschgen and Baskett 1963; Brooks 1964; Fulk and Whitaker 1969; Stewart and Sandison 1972; Bruggers 1973; Carpenter and Morrison 1973; Mahon and Aikens 1977
Spiders	Surface 1913; Frost 1935; Cohen and Howard 1958; Korschgen and Baskett 1963; Brooks 1964; Fulk and Whitaker 1969; Taylor and Michael 1971; Stewart and Sandison 1972; Bruggers 1973; Carpenter and Morrison 1973; Mahon and Aikens 1977; McAuliffe 1978
Crayfish	Holbrook 1842; Beard 1904; Surface 1913; Wright 1920; Frost 1935; Raney and Ingram 1941; Baker 1942; Penn 1950; Korschgen and Moyle 1955; Bush 1959; Korschgen and Baskett 1963; Schroeder and Baskett 1965; Fulk and Whitaker 1969; Culley and Gravois 1971; McLeran 1971; Taylor and Michael 1971; Minton 1972; Corse and Metter 1980
Snails	Holbrook 1842; Frost 1935; Raney and Ingram 1941; Perez 1951; Korschgen and Moyle 1955; Cohen and Howard 1958; Korschgen and Baskett 1963; Brooks 1964; Fulk and Whitaker 1969; Bruggers 1973; Mahon and Aikens 1977
Salamanders	Frost 1935; Cohen and Howard 1958; Fulk and Whitaker 1969; Lee 1969; Bruggers 1973
Tadpoles	Dyche 1911; Perez 1951; Cohen and Howard 1958; Korschgen and Baskett 1963; Fulk and Whitaker 1969; Culley and Gravois 1971; Minton 1972; McAuliffe 1978; Ehrlich 1979
Frogs	Downman 1883; Beard 1904; Dickerson 1906; Dyche 1911; Surface 1913; Holmes 1928; Smith 1934; Frost 1935; Raney and Ingram 1941; Baker 1942; Perez 1951; Korschgen and Moyle 1955; Jameson 1956; Martof 1956; Holman 1957; Cohen and Howard 1958; Smith 1961; Korschgen and Baskett 1963; Brooks 1964; Fulk and Whitaker 1969; Culley and Gravois 1971; Taylor and Michael 1971; Minton 1972; Stewart and Sandison 1972; Carpenter and Morrison 1973; Smith 1977; McAuliffe 1978; Bruneau and Magnin 1980*b*; Corse and Metter 1980
Fish	Beard 1904; Dyche 1911; Wright 1920; Frost 1935; Raney and Ingram 1941; Cohen and Howard 1958; Korschgen and Baskett 1963; Brooks 1964; Fulk and Whitaker 1969; Culley and Gravois 1971; Taylor and Michael 1971; Bruggers 1973; Carpenter and Morrison 1973; Mahon and Aikens 1977; McAuliffe 1978; Corse and Metter 1980
Small alligator	Beard 1904; Wright 1920; Smith 1934; Frost 1935
Small turtles	Dickerson 1906; Frost 1935; Korschgen and Baskett 1963; Schroeder and Baskett 1965; Fulk and Whitaker 1969; McLeran 1971; Taylor and Michael 1971; Minton 1972; Bruggers 1973; Carpenter and Morrison 1973; Corse and Metter 1980
Lizards	Korschgen and Baskett 1963
Snakes	Fowler 1906; Wright 1920; Baker 1942; Minton 1949; Korschgen and Baskett 1963; Brooks 1964; Fulk and Whitaker 1969; McLeran 1971; Taylor and Michael 1971; Minton 1972; Carpenter and Morrison 1973; Smith 1977; McAuliffe 1978; Corse and Metter 1980

Table 1. *Continued.*

Food	References
Shrew	Brooks 1964
Moles	Heller 1927; Smith 1934; Raney and Ingram 1941; Pine 1975
Mice	Beard 1904; Fowler 1906; Frost 1935; Korschgen and Moyle 1955; Cohen and Howard 1958; Korschgen and Baskett 1963; Brooks 1964; Schroeder and Baskett 1965; Minton 1972; Bruggers 1973; McAuliffe 1978; Corse and Metter 1980
Bats	Beard 1904; Korschgen and Baskett 1963; Lee 1969; Kirkpatrick 1982; D. Lanning (personal communication)
Birds	Dickerson 1906; Hartman 1906; Wright 1920; McAtee 1921; Smith 1934; Frost 1935; Baker 1942; Hewitt 1950; Howard 1950; Cohen and Howard 1958; Schroeder and Baskett 1965; McLeran 1971; Taylor and Michael 1971; Carpenter and Morrison 1973; Black 1974; Jacob and Pulich 1978; McAuliffe 1978

insects, followed (in order of abundance) by crayfish, snails, ranid frogs, and a variety of other terrestrial and aquatic animals (Bruggers 1973). Fulk and Whitaker (1969) examined the stomachs of bullfrogs in three habitats in Indiana, where a great variety of food was eaten. Crayfish were important at all three sites, but in the river habitat, various beetles were most important; in farm ponds, tadpoles (*Rana*) were the main food; and in a strip-mining pit, crayfish were the principal food.

In an area containing three sympatric species of *Rana*, only the bullfrogs preyed on other frogs as the

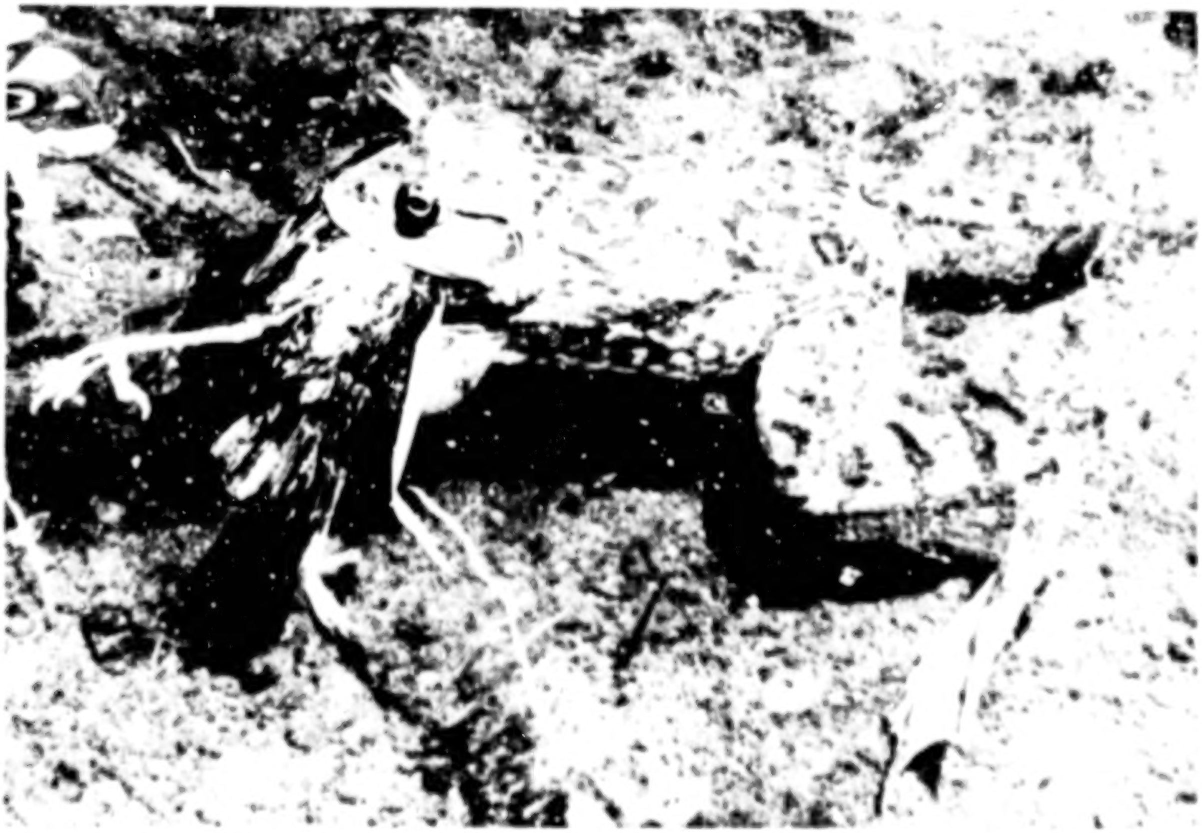

Fig. 4. Bullfrog swallowing a bird, probably a juvenile red-winged blackbird (*Agelaius phoeniceus*). *Photo by J. H. Black.*

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Table 2. *Times of emergence of bullfrogs.*

Locality	Time (month)	Reference
Louisiana	Active all year	George 1940
Gulf Coast	January	Viosca 1931
Central California	January	Storer 1925
Southern California	February	Sloan 1964
Kansas	February	Smith 1950; Collins 1974
Kansas	February–March	Collins 1982
Florida	February	Anon. 1936
Texas	February	Dawson 1953
California	March	Pickwell 1947
Colorado	March	Hammerson 1982*a*
Texas	March	Baker 1942
Missouri	March	Willis et al. 1956
Ohio	March	Walker 1946
Southeastern California	April	Storer 1925
Illinois	March–April	Durham and Bennett 1963
Indiana	April–May	Minton 1972
New York	April–May	Wright 1920

major part of their diet (Stewart and Sandison 1972). In northeastern Kansas, as much as 80% (by volume) of the food eaten by bullfrogs consisted of smaller frogs (Smith 1977). In Texas, Taylor and Michael (1971) found that crayfish constituted the main food from March through July whereas amphibians made up the bulk of the diet in August and September. Crayfish constituted 60% of the food volume in open habitats, and 40% in wooded habitats. These Texas bullfrogs would gorge themselves on crayfish and amphibians when these were available; when not available, they consumed a significantly reduced volume of food. Reptiles, insects, and miscellaneous invertebrates made up the remainder of their diet, and little month-to-month variation occurred in insect consumption. In north-central Texas, insects made up 92% of the bullfrog diet and crayfish were of minor importance (Carpenter and Morrison 1973). In southwestern Oklahoma, Tyler and Hoestenbach (1979) found feeding differences between bullfrogs from pond and stream habitats. Insects were the most important food eaten by pond-dwelling frogs (82% of total food weight), and crayfish were most important to stream-dwelling frogs (73% of weight). Fish and amphibians were also found in the stomachs of both pond- and stream-dwelling frogs. Of the insects eaten, beetles predominated.

Not surprisingly, the size of food eaten is proportional to the size of the individual frog. Quebec bullfrogs between 45 and 65 mm long ate mainly insects, whereas larger adults ate frogs, tadpoles, crayfish, and fish (Bruneau and Magnin 1980*b*). In Nebraska, newly metamorphosed frogs ate insects and spiders, 1- to 2-year-old frogs consumed mostly crayfish, and the older age classes fed on newly metamorphosed bullfrogs, bullfrog tadpoles, crayfish, and fish (McAuliffe 1978). In a Texas study, as the size of frogs increased, the occurrence of vertebrates in the diet increased and that of insects decreased (Carpenter and Morrison 1973).

Also in Texas, Taylor and Michael (1971) found that bullfrogs fed on toads (family Bufonidae) during March and April. Otherwise, *Bufo* have rarely been found in the diets of bullfrogs (Brown 1974), and adult *Bufo* are thought to be unpalatable to the bullfrog (Brown 1974; Tucker and Sullivan 1975). On several occasions, Tucker and Sullivan (1975) observed bullfrogs swallowing both adult *Bufo woodhousei fowleri* and *B. a. americanus*, and then quickly regurgitating them. The frogs apparently suffered no ill effects. However, Brown (1974) reported that the paratoid (poison gland) secretions of adult *B. woodhousei* and *B. valliceps* can immobilize large bullfrogs.

Seasonal Activities and Movements

Bullfrogs are the last North American ranid frog to emerge in the spring (Viosca 1931; Smith 1934; Ryan 1953). Emergence in northern parts of the range depends on local weather conditions and usually occurs when air temperatures are around 20–24°C and water temperatures are higher than 14°C (Willis et al. 1956; Treanor and Nichola 1972). Time of emergence follows a general northward progression, and frogs in the deep South may be active all year (Table 2).

The highest level of seasonal activity for South Carolina bullfrogs is in the spring, and terrestrial activity is positively correlated with precipitation throughout the year (Gibbons and Bennett 1974). Bullfrogs are notably less cold-tolerant than most frogs (Moore 1942;

Fitch 1956). Low temperatures probably limit the northern distribution of bullfrogs, primarily by curtailing the duration of seasonal activity (Lotshaw 1977). In fall adult bullfrogs may disappear before frosts begin, whereas juveniles may be found until freezing weather occurs (Willis et al. 1956). Bullfrogs usually hibernate during the winter and are torpid under water (Smith 1934, 1950; Willis et al. 1956; Minton 1972; Treanor and Nichola 1972; Collins 1974). However, Bohnsack (1952) found a bullfrog hibernating on land, buried under leaf litter in a 63.5-mm-deep soil pocket. Bullfrogs may hibernate by burying themselves in surface mud and may construct protective pits similar to those found for hibernating leopard frogs (*Rana pipiens*; Emery et al. 1972), or they may dig cave-like holes underwater for hibernation sites (Ruffner 1933).

Movements of bullfrogs seem to be limited. In Missouri, Willis et al. (1956) found that only 8% of the tagged bullfrogs in their study moved from one pond to another within a summar, but these few frogs traveled 0.16-2.8 km. Movements of bullfrogs seem to be highly variable; some frogs remain at one site all summer, whereas others move 150-300 m (rarely more) during a summer (Raney 1940; Ferguson et al. 1968). Movements increase during the breeding season (D. D. Cully, personal communication). Overland movements occur mostly on warm, rainy nights (Raney 1940; Gibbons and Bennett 1974). Bullfrogs probably do not migrate to any appreciable extent except during drought or other adverse conditions (Jameson 1956). When ponds dry up in California, bullfrogs seek refuge in nearby wells, springs, and crevices in the ground (Cohen and Howard 1958).

Daily Activities and Behavior

Bullfrogs have been described as primarily nocturnal (Raney 1940; Breckenridge 1944), but Jaeger and Hailman (1973) found them to be active and to feed both day and night. In Texas, Carpenter and Morrison (1973) reported no difference between the number of diurnal and nocturnal items eaten by bullfrogs, and concluded that bullfrogs feed throughout the day and night. Bullfrogs are among the most aquatic frogs in North America and spend days and nights in or along the edges of waterways. Bullfrogs desiccate at a rate similar to that of other frogs, but apparently become more stressed when desiccated than do other species because they are unable to tolerate much loss of body water (Thorson and Svihla 1943; Thorson 1956). This may account for their presence only in permanent water and their infrequent terrestrial activity. In open, muddy areas, juvenile bullfrogs sometimes excavate pits, which may conceal them or aid in preventing desiccation (Thrall 1971).

Ranid tadpoles seem to prefer the color green and tend to congregate around green plants which may offer food and shelter from predation (Jaeger and Hailman 1976*b*). Adult bullfrogs tend to move toward blue more than other colors and the response is based on true color vision (Chapman 1966; Jaeger and Hailman 1976*a*). Bullfrogs are monotonically photopositive (the mean response rate increases with increase in illumination), i.e., the species faces light. This offers several adaptive values for the bullfrog. Jaeger and Hailman (1973) suggested that because the vegetation canopy would be broken over a large body of water, jumping toward high intensity light would enable the frog to proceed quickly in the direction of water and escape predation. Furthermore, they hypothesized that it may be advantageous for a photopositive species to face an illuminated area because its prey would be more visible to it, but it would be less visible to the prey and to its own predators.

When disturbed, bullfrogs retreat to deeper water with a series of long leaps and considerable splashing (Dickerson 1906; Smith 1961). They seem to orient to local surroundings and may repeatedly use the same avenues of escape (Ferguson et al. 1968). Hobson et al. (1967) suggested that the bullfrog has a state of rest characterized by alertness but not by loss of reactivity, permitting it to effectively avoid predators or catch prey.

Bullfrog tadpoles perceive temperatures and select environments of relatively warm temperatures (24-30°C), which may increase the growth rate of individuals (Brattstrom 1962, 1963; Lucas and Reynolds 1967). They may aggregate in large numbers, probably because of thermal or other biotic or abiotic factors rather than biosocial mutual attraction (Wassersug 1973).

Transformed bullfrogs thermoregulate by changing their locations and postures, and moving in and out of water according to preferred temperatures (Brattstrom 1963; Lillywhite 1970). Bullfrogs operate at relatively high body temperatures of 26-33°C (mean = 30°C) and they are capable of exposure to insolation all day if a source of moisture is available (Lillywhite 1970). Calling of bullfrogs commences when air temperatures are above 21°C (Fitch 1956). Once started, southern Louisiana bullfrogs will continue to call when air temperatures are as low as 10°C (D. D. Culley, personal communication). Present evidence suggests that bullfrogs seek warmth and are most active at high body temperatures.

Spatial Relations and Home Range

As a measure of home range size, Currie and Bellis (1969) determined that the mean activity radii of bullfrogs in an Ontario pond was 2.6 m. Their data suggest that the home range sizes of bullfrogs may be reduced at higher densities, larger-sized frogs have bigger home ranges (also noted in green frogs, *Rana clamitans*, Martof 1953*a*), and males occupy larger home ranges than females. Although Raney (1940) found little evidence of homing in a New York population of bullfrogs, other workers (McAtee 1921; Durham and Bennett 1963; Schroeder and Baskett 1965) indicated that some bullfrogs show a homing tendency.

Although bullfrogs are usually solitary, they sometimes form breeding choruses (Dickerson 1906; Smith 1934; Wright and Wright 1949; Smith 1961; Ferguson et al. 1968). During the breeding season, ranid frogs frequently call from a particular station (on an object or floating) and exclude intruders from this site (Smith 1934; Wright and Wright 1949; Martof 1953*a*, 1953*b*; Smith 1961; Emlen 1968). Bullfrogs occupying stations float high in the water, whereas females and other males (often non-calling) keep a low profile and hence do not elicit attack (Emlen 1968). Male bullfrogs issue a specific call before defending their areas (Goin and Goin 1962; Capranica 1968; Wiewandt 1969). Males engage in combat; they wrestle, shove, and pounce on one another (Blair 1963; Durham and Bennett 1963; Capranica 1968; Emlen 1968; Wiewandt 1969). The territorial boundaries are not stationary, but males defend and exclude intruders from 3 to 25 m of shoreline (Emlen 1968; Wiewandt 1969).

Adult bullfrogs employ celestial cues (i.e., sun, moon, and stars) to orient to home shorelines (Ferguson et al. 1968). Larvae undergo orientation changes as they mature. Tadpoles tend to move toward deep water until just before transformation when their depth preference is reversed (McKeown 1969; Goodyear and Altig 1971). Tadpoles can perceive linearly polarized light and can use it as a cue in spatial orientation (Auburn and Taylor 1979). The orientation ability is of importance to physiological functions and to predator escape. Larval bullfrogs perceive their sun cues extraocularly for both sun-compass orientation and synchronization of their biological clocks (Justis and Taylor 1976), which is important for learning specific shoreline associations and for movements to and from shore.

Vocalizations are relatively well developed in bullfrogs. Both sexes may vocalize, but the mating call of the male is the loudest vocalization. The deep bass boom of male bullfrogs is often heard during warm weather (Dickerson 1906; Viosca 1931; Smith 1934; Minton 1972). The call sounds like "Jug-o'-rum," "More rum," "Br-wum," or "Be drowned." Vogt (1981) stated, "the term 'jug-o-rum, jug-o-rum' has often been used to characterize their call, but having heard hundreds of them and having a particular fondness for rum I have still not been able to equate the two." The vocal repertoire of bullfrogs consists of seven distinct types of calls: mating call by male only; territorial calls (three types—male, female, and both sexes); release calls produced by both sexes when clasped by a male; warning call, given before an escaping leap into the water; and a piercing distress call (both sexes) made with an open mouth and lasting 1-5 s (Capranica 1968). Hoff and Moss (1974) recorded another distress call, which is a scream produced with the mouth closed and lasting up to 9 s. Dickerson (1906) noted that "the scream of distress is so penetrating, and so prolonged, that we hasten to release the frog, for fear our neighbours will accuse us of cruelty to children."

Smith (1977) reported that a distress call in juvenile bullfrogs and leopard frogs attracted adult bullfrogs, which seemed to be in an excited state and attempted to feed on all moving objects (including rolled dirt clods, small frogs, other adults, and the wriggling fingers of the investigator). It was suggested that the large bullfrogs responding to the distress call might get a meal, whereas the selective value of the distress call by small frogs may be in allowing their escape from another predator due to the interference of the larger bullfrogs.

Species Interactions

Bullfrogs are often the dominant species in aquatic habitats such as canals, reservoirs, marshes, and other permanent water (Wright and Wright 1949; Korshgen and Baskett 1963; Moyle 1973). In South Carolina, the bullfrog constituted only 4.5% of the frog population in a permanent pond and 0.9% in a temporary pond (Gibbons and Bennett 1974). Nevertheless, because of its large body size, the biomass of the bullfrog is an important component of aquatic ecosystems.

Stewart and Sandison (1972) reported habitat preferences by three species of *Rana* in New York: bullfrogs occurred primarily along water margins but sometimes in the water far from shore. At this site, mink frogs (*R. septentrionalis*) were more aquatic than bullfrogs, whereas green frogs (*R. clamitans*) occupied areas along the water margins and moved inland more often than did bullfrogs.

Bullfrogs apparently have eliminated or greatly reduced the population of Vegas Valley leopard frogs (*R. pipiens fisheri*=*R. onca*) in Nevada and, in conjunction with man-caused alterations, have displaced the red-legged frog (*R. aurora*) and depleted populations of the yellow-legged frog (*R. boylii*) in the Sierra Nevada foothills of California (Moyle 1973; Cohen 1975). Introduced bullfrogs are competitively dominant over leopard frogs and spotted frogs (*R. pretiosa*) in the Bitterroot Valley of western Montana (Black 1969) and have eliminated or are eliminating native leopard frogs (*R. pipiens* and *R. blairi*) from some areas of eastern Colorado, probably through competition and predation (Hammerson 1982*a*, 1982*b*). Bullfrogs introduced into the Pacific Northwest have eliminated other ranids from many breeding ponds and have markedly decreased the numbers of western spotted frogs west of the Cascades (Dumas 1966). Jameson (1956) reported that bullfrogs had eaten all of the Pacific tree frogs (*Hyla regilla*) from one mill pond and had generally reduced this species in Oregon.

In Oregon, Storm (1952) found a bullfrog in amplexus with a red-legged frog. Fertile hybrids of bullfrog × green frog have been experimentally produced in the laboratory (Elinson 1981), but it is not known whether this hybridization occurs in nature.

Reproduction and Growth

Breeding

Geographic location greatly influences the body size and size at sexual maturity of bullfrogs. Several authors reported maturity at 85-105 mm body length (Wright 1932; Raney and Ingram 1941; Wright and Wright 1949; Ryan 1953; Treanor and Nichola 1972). In Quebec, however, sexually mature frogs measured 95-110 mm (Bruneau and Magnin 1980*b*), and in Nebraska no mature frogs were less than 115 mm long (McAuliffe 1978). In Missouri, females usually do not contain eggs until they are more than 125 mm long (Willis et al. 1956), and male bullfrogs become sexually mature at a body length of about 120 mm in the second full season after transformation (Schroeder 1975). Sexual maturity of females and males usually occurs in 2 years (George 1940, Ryan 1953), but some may become mature in about 1 year (Turner 1960). In New York, females and males are mature 2-3 years after transformation (Raney and Ingram 1941).

In general, a minimum size must be reached before frogs become sexually mature; environmental (local) factors determine the rate of growth (Porter 1972). For example, captive male bullfrogs only 2 to 4 months old and 32 g in weight had mobile sperm and some females 4 to 6 months old had eggs approaching maturity (Culley and Gravois 1971; D. D. Culley, personal communication).

Bullfrogs emerge in the spring, but the exact time depends on latitude (Table 2); earliest emergence generally occurs in the South. The breeding season (Table 3) in the northern United States lasts from late spring to midsummer, whereas in the South the season begins in March and may last as long as 9 months (Willis et al. 1956; Wright and Wright 1949; Treanor and Nichola 1972; Mount 1975). Howard (1978*a*) found that mating activity was not continuous during the breeding months; rather, activity occurs during two or three distinct periods. Only females at least 2 years past metamorphosis mate during the early breeding period. Younger females may mate in the later periods, and 1-year-old males may join later choruses. The reproductive span of adults is unknown, but probably extends over many years.

Calling males apparently attract females. Males arrive at ponds first and begin calling at stations, whereas the females remain along the shoreline until they become sexually receptive (Noble 1931; Emlen 1976, 1977; Howard 1978*a*; McAuliffe 1978; Ryan 1980).

Several authors have described different bullfrog

Table 3. *Breeding seasons of bullfrogs*

Locality	Time (month)	Reference
South Louisiana	March-September	D. D. Culley, personal communication
North Louisiana	May-August	D. D. Culley, personal communication
Texas	March-October	Blair 1961
Alabama	March-August	Mount 1975
California	April-late July	Storer 1933
Missouri	April-late July	Willis et al. 1956
Illinois	Late April-August	Smith 1961
Kansas	Late April-mid-July	Collins 1982
Indiana	Late May-late July	Minton 1972
Ohio	Late May-late July	Bruggers and Jackson 1974
Colorado	Late May-August	Hammerson 1982*a*
New York	Late June-late July	Wright and Wright 1949, Wright 1920
Iowa	July-early August	Bagnara and Kollros 1956
Nebraska	Late May-late July	McAuliffe 1978
Michigan	June-July	Howard 1978*a*
Michigan	Late May-July	Emlen 1976
Wisconsin	June-mid-July	Vogt 1981
Quebec	Late May-mid-July	Bruneau and Magnin 1980*b*

mating strategies. Emlen (1976) compared bullfrog mating systems with those of lek-breeding birds, in which males defend positions in a well-defined arena that is unrelated to any resource. The purpose of the territory is to attract females; oviposition takes place outside the chorus area, off the males' territories. Howard (1978*a*) described three male mating strategies: territoriality, opportunism, and parasitism. Territorial males (the oldest and largest animals) called and actively defended their areas from other males. Bullfrogs of intermediate age and size were opportunistic: they called but did not defend their calling sites. Parasitism was employed by the youngest, smallest males, that did not call or defend areas, but stayed close to a territorial male (often as close as 1 m away) and tried to intercept females. The older, larger males controlled oviposition sites judged to be of high quality based on their preference by females and low percentage of prehatching embryo mortality. Ryan (1980) described bullfrog reproductive strategy as "resource defense polygyny." Males defended territories and females selected mates and oviposited in the males' territories.

Amplexus occurs in the water; there is no nest construction (Emlen 1977). Eggs are deposited in a thin film on the surface of the water, usually around bushy material and at various water depths (Smith 1934; Wright and Wright 1949; Porter 1972). The number of eggs per female varies from about 1,000 to more than 25,000 (Smith 1934, 1947; Viosca 1934; U.S. Fish and Wildlife Service 1944; Wright and Wright 1949; Schroeder and Baskett 1965; Collins 1974; Vogt 1981). Collins (1982) stated that females may lay up to 40,000 eggs. In Quebec, Bruneau and Magnin (1980*b*) found that the number of eggs (3,826–23,540) depends on the size of the female. Likewise, McAuliffe (1978) reported 16,640 eggs in a female 128 mm long, and 47,840 eggs in a female 179 mm long in Nebraska, and Howard (1978*b*) reported significantly larger clutches in larger females (6,000 to more than 20,000).

The egg mass covers about 0.5-1 m² and the large surface area increases the probability that each embryo will obtain sufficient oxygen for normal development (Viosca 1931; Porter 1972). The eggs hatch in 3–5 days. Egg deposition usually occurs in midsummer in northern populations. Bullfrog eggs need higher temperatures (15–32°C) and longer time to develop than other North American frogs; their narrow embryonic temperature tolerance is correlated with the small variation of water temperature in their breeding ponds (Moore 1942). When water temperatures exceed 32°C, embryos develop abnormalities and when temperatures reached 35.9°C the embryos die (Howard 1978*a*). Ryan (1978) found that the egg mass maintains a temperature slightly lower than that of the surrounding water, thus buffering the effects of temperature increases.

In Ohio, bullfrogs undertake two major spawning efforts: one from late May to early June, and one in late July (Bruggers and Jackson 1974). In Michigan, some females arrive and lay eggs early in the season and again about 3 weeks later (Emlen 1977). But only older females (in their second year past metamorphosis and, therefore, longer than 130 mm) produced a second clutch, which contained significantly fewer and smaller eggs than the first (Howard 1978*b*). Nevertheless, the reproductive potential of bullfrogs may be exceptionally high. The double clutch is perhaps widespread in bullfrogs, especially in areas with a long breeding season, and increases the reproductive options for the species. There is no known parental care of eggs, tadpoles, or juvenile frogs. In fact, adults are often cannibalistic.

Growth

Hatchling tadpoles reach body lengths of about 26 mm by midsummer and 32 mm by November (Willis et al. 1956; Bruggers and Jackson 1974). Tadpoles may undergo differential growth rates with rapid and slow growth phases (Bruggers and Jackson 1974). Their rate of growth is related to oxygen levels, food availability, and water temperature (Rugh 1934; George 1940; Raney and Ingram 1941; Licht 1967; Bruggers and Jackson 1974).

In nature, bullfrog tadpoles transform at varying rates with a general trend of shorter time in the tadpole stage in warmer regions (Table 4). Three main factors seem to be responsible for the occurrence of an overwintering population of larval frogs: abiotic factors correlated with climatic variation that affect length of growing season; biotic factors that negatively or positively affect growth rates of individual larvae; and variation in the timing, duration, and number of annual breeding periods (Collins 1979). The number of winters a bullfrog remains a tadpole varies from none in the southern United States to one or more farther north (Hedeen 1975). Growth is decreased in winter (Hedeen 1975; Viparina and Just 1975), probably because of lower temperatures (Brattstrom 1962).

Overcrowding of tadpoles may result in retarded growth rate, delay in metamorphosis, shorter life, and decreased reproduction (Rugh 1934; Lynn and Edelman 1936; Richards 1958; Thrall 1972). Adolph (1931) proposed that increased motility and reduced space per individual of crowded tadpoles inhibited their rates of growth. Rose (1960) and Licht (1967) found that tadpoles of the bullfrog and other ranid species produce an inhibitory material that works both intraspecifically and interspecifically, and they suggested that the most severe competition in frogs occurs during the tadpole stage.

Table 4. *Time to transformation of bullfrog tadpoles.*

Locality	Time (year)	Reference
Missouri	0.2-1.0	Seale 1973
Kentucky	0.3-1.0	Viparina and Just 1975
North Louisiana	0.5-1.0	Viosca 1931
South Louisiana	0.3-1.0	Ruffner 1933
Kansas	0.3-1.2	Collins 1982
Hawaii	<0.5	McKeown 1978
Louisiana	0.5	George 1940
California	0.5	Cohen and Howard 1958
Missouri	0.5	Schroeder and Baskett 1965
Florida	1.0	Anon. 1936
Kentucky	1.0	Cecil and Just 1979
Ohio	1.0	Hedeen 1975
Illinois	1.0	Smith 1961
California (most)	1.0	Treanor and Nichola 1972
Midwest and South	1.0	Moore 1949
Missouri (central and southwest)	1.0	Willis et al. 1956
Iowa	1.0	Klimstra 1949
Iowa	1.0	Bagnara and Kollross 1956
Oregon	1+	Brown 1972
Kansas	1+	Collins 1974
Ohio	1.0-2.0	Walker 1946
Ohio	1.0-2.0	Bruggers and Jackson 1974
Michigan	1.0-2.0	Collins 1979
Indiana	1.0-2.0	Minton 1972
Kansas	2.0	Smith 1934, 1950
Illinois	2.0	Durham and Bennett 1963
Minnesota	2.0	Breckenridge 1944
Wisconsin	2.0	Vogt 1981
British Columbia	2+	Carl 1945
New York	2.0-3.0	Wright 1920
Quebec	2.0-3.0	Bruneau and Magnin 1980*a*
Nova Scotia	3.0	Bleakney 1952

In northern populations, transformed bullfrogs may grow 32-54 mm in 1 year and may double their size in the first season of life on land (Raney and Ingram 1941; Ryan 1953; Durham and Bennett 1963). The growth rate is even faster in southern populations (D. D. Culley, personal communication). Variable growth rates occur during the first few months after transformation (Raney and Ingram 1941; Turner 1960; Durham and Bennett 1963; Culley 1973). Bruneau and Magnin (1980*b*) measured bullfrogs in Quebec and found the following average snout-vent lengths: 59 mm at 1 year of age, 81 mm at 2 years, 108 mm at 3 years, 125 mm at 4 years, 137 mm at 5 years, and 143 mm at 6 years. Growth rate was most rapid between ages 2 and 3, when bullfrogs reach sexual maturity. In Missouri, Schroeder and Baskett (1968) found no differential growth in the sexes, and that the ranges of mean sizes (in millimeters) of bullfrogs were 102-104 at 1 year, 121-129 at 2 years, 130-136 at 3 years, 138-145 at 4 years, 150-155 at 5 years, and 156-175 at 6 years or more.

In nature, the growth rate is 9-18 mm a year in frogs older than about 4 years (Raney and Ingram 1941; Treanor and Nichola 1972). Wright (1920) reported that transformed bullfrogs require 5 to 6 years to reach a length of 150 mm. Bullfrogs from the northern United States may be 120 mm long 4 years after hatching (2-3 years since transformation) whereas in the South this size may be reached in 1½ to 2 years after hatching (George 1940).

Population Ecology and Trends

General Demography

Natality and mortality, and the attendant age composition of frog populations, are difficult to ascertain and there are few quantitative studies of these features for any frog (Turner 1962). The survival rates of larvae are virtually unknown and are subject to wide yearly fluctuations in north temperate climates (Turner 1962).

In Kentucky, three populations of tadpoles had survival rates of 11.8, 13.1, and 17.6% (Cecil and Just 1979); these rates were controlled by predation—not by physical factors or food availability.

Growth marks in the pterygoid bones of bullfrogs permit age-specific data analysis of populations (Schroeder and Baskett 1968) and the eye lens weight is related to age in tadpoles and adults up to 5 years old (Bruggers and Jackson 1974). Neither of these methods precisely determines age of individuals, but each is useful for indicating growth in age classes.

In harvested frogs in California, there were fewer males than females (1.00:1.84; Treanor and Nichola 1972). In an Illinois lake, an average of 48% males were taken over an 8-year sampling period (Durham and Bennett 1963). There was no significant difference from a 1:1 sex ratio in a large sample of Missouri frogs (Schroeder and Baskett 1968).

The majority of bullfrogs present at the end of summer in a temporary reservoir were juveniles of the current year (Cohen and Howard 1958). In Missouri, age distribution in frogs 1 to 6 years old varied with local conditions, frog habits, and hunting pressure (Schroeder and Baskett 1968). Groups under moderate hunting pressure maintained a constant percentage of older frogs, but heavily hunted populations had markedly fewer or no older individuals. One captive bullfrog lived for 16 years, but the estimated maximum age in the wild is 8-10 years (Oliver 1955; Goin and Goin 1962; Durham and Bennett 1963).

Status and Stability of Populations

Bullfrog population densities in California canals varied from 6.6 frogs (2.1 adults) to 119 (108.7 adults) per kilometer in control areas; the average number per kilometer was 20-25% less in areas used for sport and commercial harvest (Treanor 1975). Frog density in an Ontario pond was 1.3/m² in 1960 and 0.9/m² in 1961 (Currie and Bellis 1969). In a 7-ha Illinois lake, Durham and Bennett (1963) found a large fluctuation of 61 to 316 frogs (8.8-45.8 frogs per hectare) and a large yearly turnover in the population. Although bullfrogs once were abundant in Louisiana despite intensive human predation (Walker 1963), fewer bullfrogs are present there today (D. D. Culley, personal communication).

In California, not only numbers of bullfrogs but the proportion of larger frogs have declined (Treanor and Nichola 1972; Treanor 1975). The decrease is thought to be related to marshland drainage, vegetation control along canal banks, use of pesticides and herbicides, and harvesting for sport or commercial use. Baker (1942) reported that the bullfrog abundance in Texas was dwindling in the 1930's because of overhunting of adult frogs.

In recent times, American amphibian populations seem to have decreased significantly (National Academy of Sciences 1974). Gibbs et al. (1971) suggested that ranid frog populations of the United States had declined by 50% during the 1960's. The abundance of bullfrogs in the United States may decline so low that the biological supply industry will have to limit or discontinue the sale of bullfrogs (Culley and Gravois 1971).

Frog populations fluctuate markedly in response to environmental factors such as food shortage, drought, and early winter onset (National Academy of Sciences 1974), but frog populations in the United States do not appear to be rebounding. At one time bullfrogs were common in the United States and abundant despite harvesting (Dickerson 1906; Fowler 1906; Storer 1922, 1933; Baker 1942; Wright and Wright 1949). Today the status of bullfrogs seems less secure.

Marshland draining and man-made vegetation changes have greatly decreased bullfrog habitats, and pesticides, heavy metals, and other toxic substances are suspected of reducing or eliminating some populations. Furthermore, dwindling populations have suffered from overcollection (Baker 1942; Gibbs et al. 1971; Vogt 1981). For example, sport and commercial harvests have reduced California's populations in recent years (Treanor and Nichola 1972; Treanor 1975). Farm ponds, however, have increased bullfrog habitats (Willis et al. 1956), and widespread introductions have greatly expanded their range.

Disease

Bullfrogs host many bacteria (of which only a few seem to be major pathogens) and many protozoan and metazoan parasites (Holmes 1928; Reichenbach-Klinke and Elkan 1965; Gibbs et al. 1971; National Academy of Sciences 1974). Bullfrogs can be infected with the nematode *Eustrongylides wenrichi* by eating mosquitofish, and although this nematode can cause mortality in the frog (Modzelewski and Culley 1974*b*) it usually does not.

Frog septicemia (red leg disease) occurs in bullfrogs and kills many captive-raised or captive-held bullfrogs (Nace 1970; Treanor and Nichola 1972; Culley 1973; Glorioso et al. 1974; National Academy of Sciences 1974). Hibernation-like conditions seem to provide a selective advantage to species of bacteria involved in septicemia in frogs because the combination of low temperature and reduced food intake favor "colonization" of the frog intestinal tract by psychophiles (e.g., low temperature bacteria; Carr et al. 1976). Under natural hibernation conditions, antibacterial mechanisms may operate against the psychophiles (Van der Waaij et al. 1974; Carr et al. 1976). Viral diseases are also known and Lucke tumor herpesvirus is a major cause of death in some laboratory populations (National Academy of Sciences 1974). Tadpoles may be subject to large losses from bacterial or viral agents (Gibbs et al. 1971).

Predation

Bullfrogs are important food for other wildlife (Dickerson 1906; Wright 1920; Holmes 1928; Oliver 1955; Smith 1961; Storer 1965; Shirer and Fitch 1970; Gibbs et al. 1971; Treanor and Nichola 1972; Treanor 1975). Bullfrog eggs can be eaten by predators (leeches, aquatic salamanders, fish) with no obvious detrimental effects to the predator (Licht 1969). However, eggs and larvae of bullfrogs are distasteful to both adult *Notopthalamus viridescens* and larval *Ambystoma opacum*, two salamander predators (Nelson 1980).

Tadpoles and juvenile bullfrogs are eaten by predaceous insects, fish such as bass and pickerel, larger frogs, alligators, aquatic turtles, snakes, raccoons, skunks, mink, opossum, coyotes, otters, large waterbirds, wading birds, kingfishers, crows, owls, and hawks (Dickerson 1906; Wright 1920; Holmes 1928; Moore 1929; Viosca 1931; Fenton 1932; Raney 1940; Martof 1956; Durham and Bennett 1963; Schroeder and Baskett 1968; Terres 1968; Fraker 1970; Shirer and Fitch 1970; Vogt 1981). Adult bullfrogs are prey to larger predatory mammals and birds, and to some reptiles (Wright 1920; Holmes 1928). In a study in Nebraska, Kruse and Francis (1977) found that largemouth bass (*Micropterus salmoides*) and green sunfish (*Lepomis cyanellus*) only "maintenance-fed" on bullfrog tadpoles when these fish had no other food option, and that black bullheads (*Ictalurus melas*) chose to starve rather than feed on bullfrog tadpoles. The authors suggested that the ability of bullfrog tadpoles to coexist with potential fish predators may be due to the relatively unpalatable nature of the tadpoles.

Sensitivity to Land and Water Developments and Management

Removal of timber or brush around the edges of waterways may be detrimental to bullfrog populations. Levee construction, herbicides, and channelization are harmful to bullfrogs, as are any practices that decrease weed cover along shorelines, dry up areas of shallow backwater, or increase rates of streamflow (Soileau 1977). Draining and conversion of marshlands to agriculture, landfill, and other uses have reduced bullfrog habitat in parts of California (Treanor and Nichola 1972; Treanor 1975) and Louisiana (D. D. Culley, personal communication).

Cattle grazing seems to favor bullfrog populations in California (Moyle 1973) because construction of reservoirs, irrigation canals, and watering holes for cattle provide permanent water for the bullfrog. This is particularly critical in the plains and arid lands of the central and western United States, where most resident frogs and toads breed in temporary ponds or streams (Stebbins 1954, 1966; Conant 1975).

Bullfrogs tolerate polluted and muddy waters better than do most frogs, and may be found in stagnant streams and ponds, even within large cities (Minton 1972). They are, however, sensitive to a number of pollutants and chemicals. High carbon dioxide levels retard the rate of early cleavage of frog eggs (Merwin and Allee 1943), and large amounts of eutrophication (often with high CO_2) may stop egg development.

Ranid frogs are detrimentally affected by lampricides (Chandler and Marking 1975) and fish fungicide–parasiticides (Bills et al. 1977). Marking et al. (1977) found that frog larvae were considerably more sensitive to Furanace, a fish bactericide, than were frog eggs, invertebrates, or fish.

Herbicides containing Atrazine are suspected of killing or harming frog eggs and tadpoles (Hazelwood 1970). Atrazine concentrations as low as 0.3 mg/L significantly retarded tadpole growth in the related leopard frog (Hine et al. 1981). Fluorine concentrations as low as 1 ppm exert a constant and measurable retardation on the rate of development and stage of hatching of the frog tadpole (Cameron 1940).

Pesticides may adversely affect bullfrog populations, particularly in California and the southern United States where these agents are used extensively. There are no known recorded levels of these compounds in adult bullfrogs because of a lack of sampling. In the Sierra Nevada foothills, the yellow-legged frog had DDT residues as high as 30.8 ppm (Cory et al. 1970). Levels of DDT found in bullfrogs warrant continual testing to find out if they are acceptable for human consumption.

Hall and Kolb (1980) exposed bullfrog tadpoles to 5-ppm solutions of the organophosphorus pesticides parathion, malathion, fenthion, dicrotophos, and acephate. Tadpoles exposed to parathion and malathion showed 95 and 40% mortality, respectively. Residue levels in tadpoles contained significant bioconcentration: parathion magnified 64 times, fenthion 62 times. Thus, carnivorous animals that prey on amphibians may ingest high doses of these organophosphorus pesticides.

Slight or no mortality occurred in bullfrog tadpoles tested with 11 organochlorine pesticides at a level of 113.5 g/ha, but at 567.5 g/ha mortality was moderate to high for 9 of the 11 compounds (aldrin, endrin, dieldrin, and toxaphene were all lethal; Mulla 1963; Mulla et al. 1963). Endrin and dieldrin are among the organochlorine insecticides most toxic to adult bullfrogs (Kaplan and Overpeck 1964). Endrin is also highly toxic to cricket frogs (*Acris*) and toads (*Bufo*; Ferguson and Gilbert 1967). Ranid frogs appear to be more sensitive to DDT than are toads (Cooke 1972); they may receive a lethal dose of DDT through the skin as a result of their immersion in shallow waters where the oil-coated surface pesticide films collect (Herald 1949).

Boyd et al. (1963) suggested that natural populations of cricket frogs may be resistant to DDT because previous exposure to the insecticide has killed off susceptible individuals leaving only frogs genetically tolerant to this poison. At the same time, these authors reported that recently transformed cricket frogs were especially susceptible to DDT. Moreover, DDT levels as low as 25 ppb retarded regeneration ability in larval bullfrogs (Weis 1975). Applications of heptachlor, used to control fire ants in the southern United States, has reduced bullfrogs (Ferguson 1963).

Pesticides seem to be generally toxic to frogs. Bullfrog populations in particular are subject to exposure because they frequent farm ponds, reservoirs, canals, and permanent waters that are polluted by runoffs from agriculture lands or are unintentionally sprayed during crop dusting. Standing water also harbors mosquitos, and massive spraying programs for their control subject resident frogs to chemical compounds.

Bullfrog populations should be monitored to detect pesticide levels. The subtle, long-term effects of pesticides, particularly the toxicity levels in eggs of bullfrogs, require more critical study.

Industry has a major affect on habitat alteration and water quality, both of which affect bullfrog populations. Several studies suggest that bullfrogs are sensitive to the by-products of various industries. Water pollution includes many chemicals, biotic components, and physical disruptions. Lead salts strongly inhibit the germination of frog ova and tadpole growth at concentrations of only *N*/20,000 to *N*/100,000, whereas zinc, copper, and thallium are toxic at concentrations of *N*/50,000 to *N*/500,000 (Dilling and Healey 1926). Mining in Colorado releases acids and heavy metals (iron, copper, zinc) that seem to eliminate the resident amphibian fauna (Porter and Hakanson 1976), however, one strip-mining operation in Illinois actually provides aquatic habitat for bullfrogs (Myers and Klimstra 1963). Strip-mining in Appalachia has resulted in acid pollution, silt and sediment, and habitat disruption over large areas, and there is no evidence of reclamation designed to enhance frog populations (Boccardy and Spaulding 1968; Spaulding and Ogden 1968).

Leopard frogs exposed to aqueous solutions of copper sulfate exceeding 0.001% concentration probably will not survive, and their survival rate decreases with increases in copper sulfate concentrations (Kaplan and Yoh 1961). Fertilized eggs of leopard frogs were not affected by copper concentrations of 0.04–1.56 mg/L, but a concentration of 0.31 mg/L or more was fatal to hatched tadpoles and 0.06–0.16 mg/L measurably affected their growth (Lande and Guttmann 1973).

These studies indicate that heavy metals detrimentally affect frogs, especially the developing eggs and tadpoles. Furthermore, the eggs are sensitive to radiation, particularly in the early stages of development (Rugh 1954).

Economic Values

"Gentlemen:

The frog legs were superb. You certainly have made my entire household frog conscious. It should be a national dish" *in* Circular of American Frog Canning Co., circa 1935

Lowell Thomas

"No more succulent dish, no greater delicacy is obtainable than fresh frog legs appetizingly cooked and garnished."

(Anon. 1936)

Large numbers of bullfrogs are taken for sport or food. Frog meat is fried, boiled, or served with cream gravy as a choice entree (de Noter 1913; Hannaca 1933; Baker 1942). Some of the recipes for frog (Anon. 1936) include: Giant Frog Gumbo, Barbecued Giant Bullfrog Sandwiches, Bullfrog a la King (with mushrooms, pimento, and cream), Frog Pot Pie, Bullfrog Fondue, Frog Loaf, Giant Bullfrog Omelet, and Bullfrog Shortcakes!

The commerce in bullfrog meat is substantial. In 1976, the United States imported 2,772,578 kg of frog legs, mostly from Japan and India (National Marine Fisheries Service, *cited in* Soileau 1977). In 1971, 11 commercial collectors in California caught bullfrogs and sold them for $0.52–1.96 per pound. One supply house paid $6 per dozen. The catch varied from about 18,000 to 25,000 kg of bullfrogs per year between 1966 and 1969 (Treanor and Nichola 1972). Recent regulations have reduced frogging in California (Treanor and Nichola 1972; Treanor 1975). Latest figures show that although frog legs usually sell for $3–6 per pound, the price may reach $9–10 per pound (Culley 1981).

In the United States, researchers and educators use about 15 million frogs (including bullfrogs) annually (Culley 1973; National Academy of Sciences 1974). Bullfrogs are used for experiments in neurobiology, reproductive physiology, oncology, endrocrinology, and many other disciplines (Nace 1970; Culley 1973).

More than 10,000 bullfrogs were purchased in 1973 for educational use in 79 institutions of higher learning in California (Treanor 1975). In Louisiana, most of the wild-caught frogs are purchased by universities and research centers (Soileau 1977), which reportedly pay higher prices for frogs than do frog meat dealers.

In the western United States, introduced populations of bullfrogs have become so well established that they have moved into virtually every freshwater habitat and have eliminated many native frogs (Jameson 1956; Dumas 1966; Moyle 1973; Cohen 1975; Bury and Luckenbach 1976). Some investigators have proposed the elimination of introduced bullfrogs from areas where they threaten the survival of native frogs (Moyle 1973; Cohen 1975). Introductions of aquatic organisms have often resulted in expensive failures, and caution and restraint should pervade our present transport policies (Courtenay and Robins 1975; Magnuson 1976). Bullfrogs are already pests in many isolated waters; the introduction of bullfrogs to any new area is environmentally unsound and potentially detrimental to other economically valuable species.

Commercial Frog Culture

> the only one who makes any money from such an enterprise is the one selling the lessons or the breeding stock
>
> Karl P. Schmidt (*in* Oliver 1955)

> Bullfrog Breeders - Worlds Largest $65 pr plus handling and freight
>
> Advertisement in *Field and Stream*, 1981

Raising bullfrogs for market (bullfrog culture) once was advocated as a means for generating sizable profits and food supplies. Some of the pertinent references on frog culture include Randel (1914); Fenton (1928, 1932); Viosca (1931, 1934); Hannaca (1933); Ruffner (1933); Chase (unpublished manuscript, 1936); Baker (1942); Anon. (1952); Culley and Gravois (1970); Priddy and Culley (1972); Culley et al. (1978).

Bullfrog culture continues to be advocated, but only a few operations have had any success (Baker 1942; Culley and Gravois 1970; Priddy and Culley 1972). The requirements of bullfrogs for development to a size sufficient for market now make the raising of these frogs a highly impractical industry (Durham and Bennett 1963). Recent technology enables bullfrogs to be reared quickly and in large numbers under crowded conditions (Culley and Gravois 1970, 1971; Priddy and Culley 1972), but they must be fed well and kept clean. For example, young bullfrogs under cultivation made greater weight gains when fed mosquitofish than did groups eating crickets or earthworms, and utilized food more efficiently during the first 2 to 3 months of growth (Modzelewski and Culley 1974*a*). However, these intensive efforts by Culley and his students required culture of frogs in buildings.

Although many attempts have been made to raise frogs in outdoor ponds, Culley (1981) was not aware of any viable, profit-making operations. Labor, capital investment, and sufficient food supplies seem to be the major causes of high production costs (Culley 1981). Slow growth of frogs is also a major problem, and until larger genetic strains can be bred, the possibility of economically producing adult bullfrogs in outdoor ponds is remote (Culley 1981). Anyone seriously interested in frog-rearing should read the report by Culley (1981), which provides a comprehensive summary of the current status of bullfrog culture, analyzes rearing methods, and estimates cost.

The cultivation of bullfrog tadpoles as a protein source for humans is a novel idea, because tadpoles could be raised in a fraction of the time needed to produce adults. Martof (1955) obtained seines full of bullfrog tadpoles in Georgia and reported that they can be an appetizing food. Tadpoles may occur at extremely high densities in the wild (Ruffner 1933). A principal drawback probably would be palatability: some species of tadpoles are inedible or toxic (Licht 1969). Bullfrog tadpoles should be thoroughly tested for possible toxins. Marketability of tadpole tails or niblets is also untested. More likely, whole tadpoles could be cooked and canned for a protein source in the pet food industry. Live tadpoles might be fed to adult bullfrogs, catfish, or other "cultured" species.

Accumulating information on the ecology of frog tadpoles (Altig and Christensen 1976) is greatly increasing our understanding of this life stage. Culturing larval bullfrogs should follow many of the principles of catfish farming; e.g., warm water seems to foster rapid growth. With a diet low on the food chain, tadpoles can convert algae and detritus into high-quality protein. The "meat" of tadpoles is in the tail, which is easy to cut from the body. The tail may constitute 40% of body weight (Martof 1955), and would be easy to slice for canning or freezing. The head, intestines, or whole tadpoles can be fed to other tadpoles, catfish, or chickens.

Tadpoles decrease in weight during transformation because of anatomical and physiological reorganization (Bruggers and Jackson 1974). Thus, for maximum yield tadpoles should be harvested before metamorphosis. Horseman et al. (1976) reported that a disturbance (such as water changing) inhibited bullfrog metamorphosis. This effect could be useful in laboratory or commercial management of bullfrogs because metamorphosis might be hastened or postponed for convenience and efficiency.

Cultivation of bullfrog tadpoles is being tested with a flowing water culture system and an artificial tadpole food (Culley et al. 1977). Tadpole growth apparently is retarded by crowding. The inhibitor is unknown, but may be reduced by flowing water.

The use of tadpoles as detritus consumers may have great potential in sewage treatment processes. Nutrient-rich "wastes" cause eutrophication problems in many aquatic ecosystems. Conversion of the nutrients into biomass may be accomplished by aerating holding ponds or tanks and stocking with algae and tadpoles. Under proper conditions, the tadpoles would consume the algae and nutrient-rich wastes (Thrall 1972; Seale 1973). In turn, man could seine off the tadpole biomass at intervals and use the animals for meal or other purposes. This scenario is probably within present technological abilities.

The large tadpoles of bullfrogs require permanent water lasting at least 6 months for maturation. Faster-growing frog species would be able to mature in temporary ponds—unlike bullfrog larvae or fish. Also, the culture of local frogs would be preferable to that of introduced bullfrogs, which are potential pests. Tadpoles of some frog species probably could produce a large amount of protein by means of aquaculture; however, before frog species are selected for culture, we strongly recommend careful toxicity tests to ensure palatability.

Management of Wild Stocks

Limited cropping of frogs from natural ponds afford a means for obtaining them without expensive artificial culture (Baker 1942; Oliver 1955). Many marketed frogs are already collected in large numbers from the wild; however, this source is among the most abused. Bullfrogs are harvested throughout the United States and many States have restrictions on hunting seasons, means of capture, and size and bag limits (Durham and Bennett 1963; Czajka and Nickerson 1974; National Academy of Sciences 1974; McAuliffe 1978). However, the bullfrog is one of the few game species taken with limited or no data on annual harvest, recruitment rates, sport value, or life history. California (Treanor and Nichols 1972; Treanor 1975) and Nebraska (McAuliffe 1978) seem to be the only States monitoring populations, and these programs are sporadic.

If adequate cover is present, moderate hunting pressure is probably not detrimental to bullfrog populations, but it may reduce the proportion of adult males because their chorusing makes them conspicuous and more vulnerable than other age–sex classes during the breeding season (McAuliffe 1978). Heavily hunted populations in Nebraska contain few frogs more than 1 year old, but the high fecundity of breeders that remain can usually replace annual losses. However, McAuliffe (1978) believed that short-term drought, lowered water levels, loss of marsh habitat, and subsequent increased hunting pressure might lead to lowered survival in both metamorphic and larger adult age classes; if this continues for several seasons, local extinction may occur. Furthermore, bullfrogs cannot be collected as intensively as many species of frogs because of the long time needed for maturation to replenish the population (Vogt 1981).

Sustained yield of marketable bullfrogs requires management practices at or near the level provided for other game. Hunting seasons should be set to protect adult bullfrogs before and during the breeding season, preferably starting hunts after mid-July (Wright 1920; Baker 1942). McAuliffe (1978) recommended a minimum length restriction of 115 mm to allow most of the bullfrogs at least one season for reproductive opportunity; he also recommended using capture methods that allow small frogs to be released unharmed. Suggested methods include hand capture, nets, hook and line, and spring-loaded "grabbing" tongs.

Fig. 5. Bullfrog in its aquatic realm. *Photo by J. H. Black.*

Although the species has an exceptionally high potential for recovery, adequate habitat must be provided (Fig. 5). If tadpole survival is low because of predation, insufficient food, or pollution (e.g., pesticides, herbicides), then management of adults is futile.

Today bullfrogs are less common than many other frogs, probably because their large size has made them especially valuable as food for man (Dickerson 1906; Baker 1942). For such an important game species, management practices are inadequate and the population dynamics of tadpoles and newly metamorphosized frogs are poorly known. Such information is critically needed for recovery and maintenance of viable stocks of native bullfrogs.

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Bury, R. Bruce and Jill A. Whelan.
Ecology and Management of the Bullfrog. U.S. Fish Wildl. Serv., Resour. Publ. 155. 23 pp. 1984.

This paper summarizes and critically reviews information on the biology of the bullfrog related to its ecology, present status, culture, and management. Information through 1982 was selected representing the most recent, important biological and economic features of the bullfrog, and includes historic references where such information is pertinent.

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A list of current *Resource Publications* follows.

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